

The Nesting Behavior and Dynamics of *Bicyrtes angulata* (F. Smith) with a Comparison to other Species in the Genus (Hymenoptera: Sphecidae)

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Abstract.—Data are presented on the nesting behavior and dynamics of a population of *Bicyrtes angulata* (F. Smith) found on the campus of the Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil. Many aspects of the biology of this population of *B. angulata* are similar to all (or the majority) of the 8 other species in the genus that have been studied in some detail. Other features were atypical in comparison, such as: (1) nesting in sandy soil far from water (2) constructing relatively short burrows (less than 10 cm on average) (3) taking more than two hours to dig a nest. New information is presented on the level of nest failure (roughly a third of all nests initiated are not completed), mortality (roughly 90% of all completed nests fail to produce adult wasps), and variability in egg to adult developmental time (44 to 375 days) due to bimodal prepupal dormancy. Factors affecting mortality are discussed, the most important being termites and ants. The number of nests made per female varied slightly over the year, this ratio being lowest in the dry season (winter and spring), and was not correlated with the total number of nesting females, thus suggesting that there is little or no competition for nesting space in the area. Possible alternative explanations for these patterns are offered, in relation to prey abundance and female mobility and longevity, and we suggest that the availability of suitable patches for nesting may potentially be of importance in the nesting dynamics of this species.

Of the 23 described species of *Bicyrtes*, 12 are found exclusively in South America, 8 in North America and 3 occur in both continents (see Bohart and Menke 1976 for distributions; Willink, 1947, revised the South American species). Their biology is largely either unknown or poorly known, with the exception of the North American *B. quadrifasciata* (Say) (see Evans 1966 for a review). Some additional information is available for *B. discisa* (Taschenberg), *B. simillima* (Smith) and *B. variegata* (Olivier) (Genise 1979, 1982), *B. cingulata* Burmeister (Evans and Matthews 1974), and also for the Cuban *B. spinosa* (Fabricius) (Sánchez and Genaro 1992). Few of the details of nesting and provisioning behavior have proven to be uniform across all species (see Discussion). Information on addition-

al species should help address questions related to patterns of behavioral evolution within the genus.

Bicyrtes angulata (F. Smith) occurs in French Guiana, Paraguay, Argentina, and Brazil (Bohart and Menke 1976). Records for *B. angulata* in Brazil include some states in the North and Northeast (Nascimento and Overall 1980) and São Paulo (Martins 1991), but its biology has been unknown until the present, and is compared here to what has been recorded for other species in the genus. This includes novel information on prepupal dormancy, and rates and causes of nest failure and mortality.

STUDY SITE AND METHODS

We observed an aggregation of *B. angulata* (147 marked nests in 1993 and 80 in

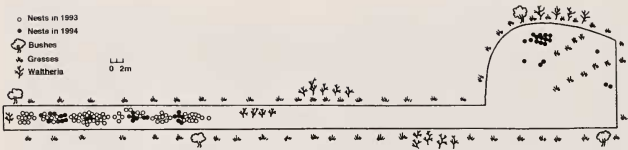


Fig. 1. Diagram of the nesting site of *Bicyrtes angulata* showing nest distributions in 1993 and 1994.

1994) on the Campus of the Federal University of Minas Gerais (UFMG), Belo Horizonte, Minas Gerais, Brazil, from January 1993 to June 1994. We spent a total of 556 hours making ad libitum and focal individual observations (*sensu* Martin and Bateson 1986), mostly between 0900 and 1200 h when the majority of nesting activity occurred, and opportunistically at the beginning and end of some days. The study site, Prefeitura, is a secondary growth, relatively undisturbed area, mostly covered with grasses, scattered bushes, and trees (including a few exotic and or-

chard species; see photo in Gaimari and Martins 1996). Nearby fields of corn, bean and manihot support a substantial population of *Waltheria americana* (Sterculiaceae), a weed whose flowers are commonly visited by *B. angulata* (Macedo and Martins 1998).

Most nests of *B. angulata* were concentrated in a 35 m long and 0.65 m wide strip of a dirt road (approx. 700 m² total) on a superficially compacted well-drained sandy soil. Nesting soil was completely free of vegetation and exposed directly to the sun (Figs. 1 and 2). We built a tem-



Fig. 2. Nesting site of *Bicyrtes angulata* showing the plastic-cup emergence traps.

porary fence around the nesting area to prevent vehicular and pedestrian traffic. In 1993 the area also contained numerous nests of other sphecoid wasps: 193 of *Rubrica nasuta* (Christ) (Pimenta and Martins unpublished data), 54 of *Ammophila gracilis* Lepeletier (Gaimari and Martins 1996), 4 of *Bicyrtes discisa*, 4 of *Trachypus* sp., and 1 of *Prionyx fervens* (Linnaeus). There were also a few bee nests at the same time: 7 of *Centris aenea* Lepeletier, and 1 of *Megachile neoanthoptera* Cockerell.

We marked and released 180 females (127 in 1993 and 53 in 1994) and 31 males (19 in 1993 and 12 in 1994) that were captured in or near the nesting site while either searching for a place to begin excavation, in the process of excavating a nest, flying in search of prey or in transit to the nest, or visiting the flowers of *Waltheria americana* (see Macedo and Martins 1998, for annual records of *B. angulata* visits to this plant). Numerous additional wasps were marked in areas outside the nesting area, but none of these wasps were subsequently encountered there. Wasps were restrained and marked individually with fast-drying non-toxic acrylic paint using combinations of 4 colored dots on the corners of the scutum, making it possible to observe individual variation in daily phenology, nesting (note that many marked females made no nests in the study site), provisioning, male behavior, longevity, interactions with other insects and plants, and movements in the aggregation and its surroundings. Adult longevity was calculated as the length of time between when a wasp was marked and the last time it was seen, and is thus likely to be a very conservative estimate, though many wasps were never seen again after marking (64 females and 21 males), and we did not include these individuals in the average. Differences between male and female longevity were tested using Student's *t*-test.

Nests were marked during interruptions in the nest excavation process, using

4 cm-long and 5 mm-wide aluminum arrows fixed to the ground with nails. Arrows were distinguished by colors corresponding to those of the resident female and/or by numbers. After observing a definitive nest closure, we nailed an emergence trap (a marked plastic cup) to the ground at the nest entrance (Fig. 2), to record egg-adult development time and the emergence of nest parasites. This also helped us to estimate the number of annual generations. Wasps from the first generation that emerged in the field or in the laboratory were marked and released in the study site, so as not to extirpate the population.

We excavated all 227 marked nests to determine their architecture and contents, assessing whether they were deserted, parasitized, destroyed by ants or termites, or completed. The status of the nests during the study was categorized as follows: (1) Deserted nests were those in which we observed a female working but which proved to be empty upon excavation (this class of nests thus includes both abandonment and female mortality events) (2) Parasitized nests were those in which parasites appeared in the emergence traps (3) Nests destroyed by ants or termites were those in which we found pieces of destroyed cocoons and prey remains (4) Completed nests were those that we observed being provisioned and in which we found all remains of cocoons and/or prey. Only nests which were not deserted were included in the analysis of nesting phenology and counts of nests per females.

We counted 307 prey that were consumed by larvae in 26 of the nests; it was possible to count the exact number of consumed prey because their heads and scuta remained intact in the cell. Eight days after provisioning ceased, seven nests were excavated to measure the time of development from egg to prepupae. The number of pores of 14 cocoons were counted and the larger and smaller diameter measured for 8 of them. We made casts of 2



Fig. 3. Architecture of the nest of *Bicyrtes angulata*.

completed nests with plaster of Paris to record their shape (Fig. 3), and casts of two incomplete nests. Nesting activity was measured as the number of nests initiated per month. We plotted the number of nesting females per month versus the average number of nests made per female to assess evidence for density-dependent effects. For quantitative measurements we calculated averages with standard deviations.

Voucher specimens of wasp and prey were deposited at the Laboratório de Ecologia e Comportamento de Insetos of the Departamento de Biologia Geral, ICB-UFMG, Belo Horizonte, MG, Brazil.

RESULTS

Nest excavation.—Over the entire study, a total of 180 females excavated 227 nests, and 80 of these females excavated at least one nest within a week of being marked. In 1993, the final nest density was approximately 16.5 nests/m². We also observed the origin of a new nest site in 1994, when 29 out of the 80 nests of *B. angulata* found were in an area close to, but separate from, the original site (Fig. 1).

Females walk in a slow and meandering path over the nesting site, occasionally antennating the ground, until they find a suitable spot (the selection criteria are unknown, but are likely to be tactile) and begin to dig. Females dig primarily with their mandibles, using the forelegs to scoop loosened soil backwards, throwing the soil out from under the body. This movement is accompanied by a rapid rocking motion of the body, lifting the ab-

domen each time the soil is thrown, and simultaneously tilting the head down over the soil. The excavated soil accumulates, forming a mound (tumulus) close to the nest entrance. Over the entire period of excavating a single nest, females spend an average of 2.26 ± 0.13 h ($n = 4$) actually digging the nest, but also 2.39 ± 0.24 h ($n = 4$) flying to and from the nests, or simply resting in the tunnel. Completed nests ($n = 5$ with all measurements taken) have a straight tunnel, 9.6 ± 1.1 cm long and 0.8 ± 0.1 cm in diameter, angled from 20° to 35° relative to the soil surface (Fig. 3), and ending in a single ellipsoid cell (only two nests had two cells) measuring 2.6 cm long by 1.2 cm in diameter (all 5 measured cells identical), at 5.6 ± 0.54 cm depth. Females typically complete nest excavation in the afternoon. Afterwards, they close the nest entrance and fly away to feed on nectar, and, from March 16 to April 20, to sleep in mixed male/female aggregations on inflorescences of *Panicum maximum* (Poaceae), in proximity to adults of *Rubrica nasuta* (described below) (Fig. 4). No form of orientation flight was ever observed, either after nest construction, afternoon closure, or in between provisioning trips.

Nest provisioning.—Out of 227 nests, 147 were successfully provisioned by 103 different females. Provisioning can occasionally start the same afternoon that nest excavation is finished ($n = 2$) but is generally begun the following day. In the latter case, by 0830 to 0900, the females return and open the nest entrances with their forelegs, using motions as described above. Hunting trips occur between 0845 and 1545 h. As they leave the nest for the first and all subsequent hunting trips, they emerge headfirst, and temporarily close the entrance by scooping the tumulus backwards into the entrance. However, sometimes nest entrances stay partially open due to careless and hasty closure. If heavy rains level off the mound, females still have little or no difficulty finding



Fig. 4. Mixed male-female sleeping site of *Bicyrtes angulata*.

their nest. Sometimes they seem confused initially, but soon find the nest entrance and reopen it.

Prey are immatures (sometimes adults) of *Megalotomus* sp. and *Apidaurus* sp. (Hemiptera: Coreidae: Alydini [=Alydidae]), accounting for 302 prey items; only one anomalous cell was found, containing 5 pentatomid nymphs. Each prey is stung and partially paralyzed, then the wasp flies back to the nest holding it venter up with her middle legs. She then removes the nest closure with her front legs, keeping the prey in the same position, and in this way she enters the nest headfirst. Once, after removing the nest closure, a female dropped the prey at the nest entrance, entered, came back out headfirst, grabbed the prey in her mandibles, and dragged it down to the cell by moving backwards. Hunting trip lengths are quite variable (45.6 ± 35.9 min., $n = 13$; range 1–95). After capturing the first prey and placing it in the nest, one egg is attached

erect on the metasternum between the middle or hind coxae, exactly as shown by Evans (1966:158). Since the time between the first and second provisioning trips can vary considerably, it appears that the egg may hatch either before or after the second prey is supplied, but in most cases it is probably after two or three prey are already in the nest.

Provisioning is progressive and somewhat lengthy, lasting approximately 6 consecutive days per nest (6.5 ± 0.53 , $n = 7$), with roughly 12 prey per completely stocked cell (11.88 ± 4.46 , $n = 26$; range 7–24). The final closure of completed nests begins with females scraping the tumulus into the nest entrance, as when making a temporary closure, but is somewhat more thorough, and this is followed by a bout of "hammering," during which a female delivers vigorous blows with the tip of the abdomen until the nest entrance is compacted and levelled. The egg-prepupa developmental period is rapid, as we found

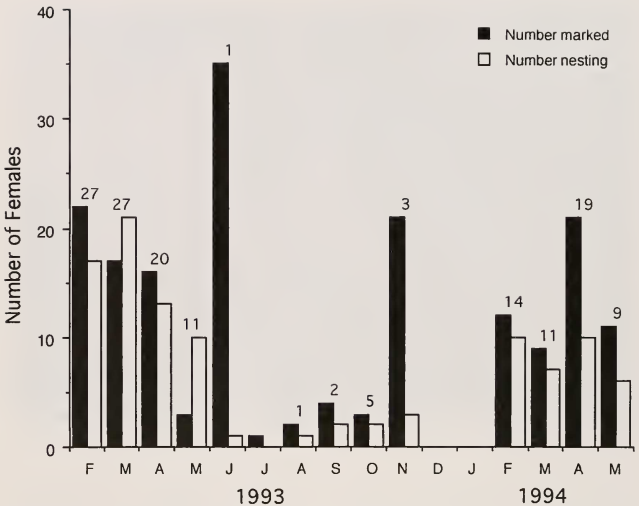


Fig. 5. Number of marked and nesting females of *Bicyrtes angulata* in 1993 and 1994. Numbers above the bars indicate the total number of nests constructed in that time interval.

prepupae already inside their cocoons ($n = 7$) when excavated 8 or 9 days after provisioning had ceased. Cocoons had 4 to 6 pores (5.5 ± 1.95 , $n = 14$) and averaged 17 ± 0.9 mm long by 5.3 ± 0.06 mm ($n = 8$) in diameter. The entire cycle for a single nest, from first excavation to final closure, typically takes 8 days (8.5 ± 0.5 , $n = 6$).

Seasonal phenology and demographic patterns.—Adults are found during the whole year, mainly visiting flowers, but nests are built mainly from February to May (mid-summer and autumn; 85 of 97 provisioned nests in 1993, and all 50 in 1994; Fig. 5). The ratio of nests provisioned per nesting female was generally higher than one except in the winter and spring (June through November, Fig. 6; in October the ratio was higher because two females pro-

visioned five nests in total). Overall, there is no relationship between the number of nesting females per month and the average number of nests per female per month. If we consider the number of nests relative to the total number of marked females, it is obvious that many females were present in the area that never made nests (in 7 of 14 months in which nesting was observed, there were more marked females alive than nests provisioned). Despite the fact that the range of number of nests per nesting female was one to seven, the average number of nests per marked female only varied from 1.0 to 1.5 in different months.

Females seem to feed on flowers in areas other than those in proximity to their nests; only three out of 77 females marked

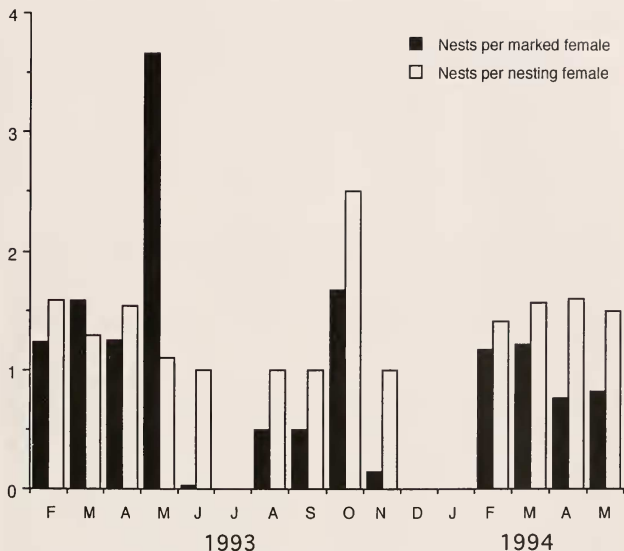


Fig. 6. Monthly ratio of number of nests to females of *Bicyrtes angulata* in 1993 and 1994.

on *W. americana*, close to the study site, were seen nesting in the aggregation. However, 77 out of 103 females that were marked while visibly searching for a place to begin excavation were later seen nesting there. Females stayed in the aggregation from 1 to 84 days (24.1 ± 17.5 , $n = 116$). One female was observed nesting until the age of 65 days, with no apparent mandibular or wing wear over this time. The estimate of male longevity (31.4 ± 20.4 days, $n = 10$; range 3–56) was not significantly different from that of females (Student's $t = -1.25$, $p > 0.2$).

There are at least 2 annual generations, though these are staggered and overlap-

ping rather than synchronized and discrete (see Table 1). The range of time from oviposition to adult emergence was 44 to 375 days (200.1 ± 137.1 , $n = 13$; Table 1). The origin of such variability is in the prepupal stage, which may remain dormant for widely varying intervals of time. This variability in dormancy can occur not only among but within the broods of individual females; two eggs from one female produced adult males after 55 and 375 days of development. The operational sex ratio at this site was apparently female biased; 15 wasps from the first generation emerged (in the field or from cocoons brought into the laboratory), of which 9

Table 1. Developmental intervals of *Bicyrtes angulata* (arranged by starting date).

Nest	Nest starting date	Nest closing date	Adult emergence date	# days egg-adult	Sex
1	12 Feb 1993	18 Feb 1993	16 Apr 1993	57	F
3	13 Feb 1993	19 Feb 1993	9 Mar 1994	375	M
2	16 Feb 1993	3 Mar 1993	27 Apr 1993	55	M
12	19 Feb 1993	26 Feb 1993	3 Feb 1994*	342	F
4	3 Mar 1993	9 Mar 1993	19 Aug 1993	163	M
10	8 Mar 1993	?	7 Feb 1994	ca. 310	F
13	17 Mar 1993	1 Apr 1993	30 Jan 1994	335	F
11	30 Mar 1993	13 Apr 1993	3 Feb 1994*	296	M
15	1 Apr 1993	13 Apr 1993	11 Apr 1994*	356	F
5	24 Apr 1993	6 May 1993	29 Jan 1994	328	F
7	1 May 1993	6 May 1993	4 Sep 1993	88	M
6	6 May 1993	?	31 Jan 1994	ca. 310	F
9	13 Oct 1993	28 Oct 1993	24 Jan 1994	88	F
8	28 Oct 1993	5 Nov 1993	24 Jan 1994	80	F
14	11 Feb 1994	22 Feb 1994	8 Apr 1994	44	M

* These individuals emerged in the laboratory.

were females (60%). We found 5.7 females per male (85% females) over the period of the study, though males were rarely seen on the aggregation and thus their abundance was likely underestimated.

Movement patterns and diel phenology.—Adults of *B. angulata* spend nights on plants. From March 16 to April 20, marked *B. angulata* and *R. nasuta* were seen sleeping on inflorescences of *Panicum maximum* (Fig. 4). The highest number of wasps seen in a single group was 17 *B. angulata* and 9 *R. nasuta* (J. F. Macedo, pers. comm.). Females leave the sleeping site between 0800 and 0830 h to take nectar prior to the start of nesting activities (other phenological data above). Usually after 1600 h, or when it is very cloudy, they return to the sleeping site. One day they left the sleeping site early, returned around 0900, but then resumed nesting activities between 0900 to 1000 h, when the sun began shining again. *B. angulata* comprised 34% of the individuals of the 29 bee and 51 wasp species visiting *Waltheria americana* between 1000 and 1200 h in April 1993 and April 1994 (Macedo 1995). The highest number of *B. angulata* seen on *W. americana* during one month was 35 females and 7 males in June 1993 at a site some distance from the nest-

ing site (despite the availability of flowers, no visits were observed on the same plants in June 1994, reflecting the large variation in the abundance of wasps between years).

Only 8 males were captured and marked (of 31 total) while they were patrolling the aggregation by flying close to the soil, continuously going back and forth. Occasionally they clashed briefly in mid-air with other males, females, or other insects flying in the patrolling area. The highest levels of patrolling activity were observed in April between 0845 to 1145 h, and 1300 to 1600 h. Despite the patrolling activity, copulation was never seen in the aggregation, nor on flowers of *W. americana* or in the sleeping site.

Four new adults were observed emerging from their cells between 1045 and 1145 h, and new adults were generally found in the emergence traps in the mornings, suggesting that there is a preferred daily emergence time.

Interactions with natural enemies and other insects.—The female actively defends the nest entrance against insects. Once, when an army ant trail crossed the entrance of one nest, the female tried to drive them out by touching them with its abdomen or

Table 2. Survivorship and success of *Bicyrtes angulata* nests.

Nest status	Number of nests per year				
	1993	1994	Total		
Marked	147	80	227		
Marked	Abandoned	46	30	76	
Marked	Cast in plaster	4	0	4	
Marked	Completed	97	50	147	
Marked	Completed	Failed	83	49	132
Marked	Completed	Survived	14	1	15

hovering above them. However, we never observed females carrying ants into the air and dropping them a few cm away, as *Ammophila gracilis* did in our study site (Gaimari and Martins 1996). A butterfly that was flying repeatedly over a nest was also driven away by the resident female; in this case the wasp hovered above the butterfly, approaching and touching it several times until it was driven off. Aerial clashes were common between males and females of *B. angulata* and *R. nasuta*. Once, a female of *B. angulata* entered a nest of *R. nasuta* while the latter was discarding a prey item not consumed by her larva, and when the *Rubrica* returned, she found the *Bicyrtes* and drove her away. A few minutes afterwards, this female started to excavate her own nest close to that of the *Rubrica*.

Table 2 summarizes the fate of the nests initiated in 1993 and 1994. Out of 227 nests, 147 were completed; 76 were abandoned and four were cast in plaster; excluding the latter, then, some 34% of nests were abandoned. Apparent causes of nest abandonment were: excavation in hard soil ($n = 8$); proximity to ant nests (2); heavy rains (2); female disturbed by a female of *R. nasuta* (1); and the remainder (63) were due to unknown causes.

Of 147 provisioned nests, only 15 produced adult wasps; 100 were destroyed by ants (principally *Solenopsis* sp.) and termites; 16 experienced immature mortality of unknown nature; 7 pupae died due to flooding of the nesting site; 6 nests were

parasitized by *Ligyra morio* (Diptera: Bombyliidae; 5 adults emerged in 5 traps); one nest was apparently parasitized by *Metopia* n. sp. nr. *sinipalpis* (Diptera: Sarcophagidae; Miltogramminae; emerged in one trap), a major parasite of *Ammophila gracilis* in the study site (Gaimari and Martins 1996); and two nests were excavated prematurely to document egg placement on prey. Excluding the latter two nests, mortality of completed nests was approximately 90%. One entire aggregation of 25 marked nests was extirpated in 1991 by ants and termites at the Ecological Station of the UFMG.

DISCUSSION AND CONCLUSIONS

The data from this study are only exceeded by those available for *B. quadrifasciata*, obtained by several workers in numerous localities in the United States (see Evans 1966 for a review). As Evans (1966) has claimed, a detailed comparison of the behavior of the species of *Bicyrtes* requires that other species like *B. angulata* are studied in detail. Following Evans' (1966) summary of features of the ethology of the species of *Bicyrtes*, we have thus confirmed some general patterns within the few members of the genus that have been studied, as well as added new information (Tables 2, 3 and 4), though, as mentioned, only a few of the details of nesting and provisioning behavior are uniform across all species.

Adults of *B. angulata* are like all the other studied species in the genus in some

Table 3. Comparison of qualitative features of *Bicyrtes* nesting biology.

	<i>angulata</i>	<i>discisa</i>	<i>variegata</i>	<i>simillima</i>	<i>quadrifasciata</i>
Provisioning	progressive	mass	mass	mass	delayed
Prey paralysis (partial)	yes	yes	yes	yes	?
Prey types*	N \geq 4 (+A)	N \geq 4	N5	N5	N
Prey families**	C	P	P	P	CPRLSCy
Foraging during morning-afternoon	yes	?	?	yes	yes
Mound (tumulus) near nest entrance	yes	yes	no	yes	no
Nests aggregated***	yes	no	yes	no	no
Accessory burrow	no	no	yes	yes	?
Sleep in accessory burrow	no	no	?	yes	?
Sleep in mixed association	yes	?	?	no	?
Citation****	present work	G1982	G1982	G1982	E1966

* N = nymphs (followed by instar numbers if specified), A = adults, (+A) indicates adults rarely taken.

** C = Coreidae (s.l.), P = Pentatomidae, R = Reduviidae, L = Lygaeidae, S = Scutelleridae, Cy = Cydnidae, Rh = Rhopalidae, Py = Pyrrhocoridae.

*** Statistics not available; category represents subjective evaluation of authors as to dispersion of nests relative to apparent available space.

**** G1982 = Genise 1982, E1966 = Evans 1966, E&M1974 = Evans & Matthews 1974, S&G1992 = Sánchez & Genaro 1992.

respects: (1) they are frequent visitors at flowers for nectar (they do not feed upon the prey they capture for their larvae) (2) they are solitary ground-nesting predators (3) prey are immature and/or adult heteropterans (4) nest closure is maintained while outside the nest (5) foraging is primarily in the morning and afternoon. Other features which appear similar to the majority of species studied include: (1) nesting in multispecies aggregations (2) sleeping on vegetation (3) partial paralysis of prey (4) nests with one or two cells (5) low nest angles (generally less than 45°).

Other features were atypical, such as: (1) nesting in sandy soil far from water (other species except for *B. spinosa* nest along water courses) (2) relatively short burrows (less than 10 cm on average) (3) more than two hours to dig a nest. The presence of a tumulus can neither be considered exceptional nor general, and for other features comparative information is lacking.

A few of these points merit further discussion. Despite the general tendency of *B. angulata*, like other species, to intersperse its nests with those of other digger wasp and bees, it tends to aggregate intraspecific

Table 4. Comparison of quantitative features of *Bicyrtes* nesting biology.

	<i>angulata</i>	<i>discisa</i>	<i>variegata</i>	<i>simillima</i>	<i>quadrifasciata</i>
Number of cells per burrow	1-2	3	2-5	1	2-3
Number of prey per cell	7-24	16	3-6	11	8-11
Time to dig cell/nest (min)	146 \pm 14	30	60	>60	60-120
Angle of entrance burrow	20°-35°	30°-35°	30°-35°	30°	30°-60°
Nest depth (cm)	5.6 \pm 0.54	5	8-10	20	?
Nest length, burrow plus cell (cm)	9.6 \pm 1.1	12	12	24	8-43
Length of cell (mm)	25-26	18-20	25-30	17	20-35
Width of cell (mm)	12-13	10-12	12-15	12	5-27.5
Number of pores in cocoon	5.5 \pm 1.95	?	5	?	?
Egg-adult developmental time (days)	44-375	?	?	?	49
Number of generations per year	2	?	?	?	?

Citations as for Table 3.

Table 3. Extended.

<i>centralis</i>	<i>foedens</i>	<i>cingulata</i>	<i>spinosa</i>
delayed	?	progressive	progressive
?	?	?	no
N	N+A	N+A	N(+A)
CPRLSCy	PS	Rh	CPLSPy
?	?	yes	yes
no	no	no	yes
variable	?	?	variable
?	?	?	no
?	?	?	no
?	?	?	no
E1966	E1966	E&M1974	S&G1992

ic nests within these areas. As in its congeners, *B. angulata* maintains an outer closure at all times when the female is not in the nest, but no inner closure is ever made. Prey are Coreidae (sensu lato), indicating in our case a possibly high level of local specialization, compared for example with the Cuban generalist *B. spinosa* that preys upon several species of five heteropteran families (Sánchez and Genaro 1992). Additionally, the prey is partially paralyzed and carried in flight with the middle legs, clasped tightly beneath the base of the wasp's abdomen, and is not usually deposited on the ground at any time. The egg is laid in a semierect position on the mid-ventral line of the first prey item. Our observations established that *B. angulata* is a progressive provision-

er like *B. spinosa* and *B. cingulata*, though mass provisioning and delayed provisioning are found in other species.

Among the novel data for *B. angulata* is the huge variability in the time of prepupal dormancy within the same brood. This variability (sometimes called "parsivoltinism"; Torchio and Tepedino 1982) is scarcely documented for Nearctic and Neotropical species of solitary wasps and bees (see Evans 1966; Stephen et al. 1969; Evans and West-Eberhard 1970; Torchio and Tepedino 1982; Roubik 1989; Wcislo and Cane 1996). A comparable variability was also found for other species of solitary wasps and bees in the same study site or in other sites in the Ecological Station of the UFMG (Martins et al. 1996; Almeida et al. 1997; Pimenta and Martins unpublished data). One of the possible interpretations for such a pattern is given by theories of risk spreading of reproductive effort (or "bet-hedging") in unpredictable environments (Danks 1987; Tauber et al. 1986). The possibility that parsivoltinism may help avoid predation or parasitism in some way seems reasonable, but we cannot confidently identify the precise mechanism of selection for such an adaptation in the present case. We do believe, however, that we can exclude variability in the occurrence of rains (as in deserts where similar insect life cycles occur, e.g. Hanski 1988), because our study site is strikingly seasonal and predictable in the occurrence of rains (see Martins and Antonini 1994) and dormancy seems to not correlate with rains (R. P. Martins unpublished data).

There is an apparent paradox in the data on number of marked females versus number of nests made (see Fig. 5). Many marked females visiting flowers at the study site did not nest there, so the total number of females exceeded the number of nests in 7 of the 14 months when females were present. Why are there so many active females that are apparently not nesting? This same phenomenon occurs in *R. nasuta* (Pimenta and Martins un-

Table 4. Extended.

<i>centralis</i>	<i>foedens</i>	<i>cingulata</i>	<i>spinosa</i>
1-2	2-5	1	1
3-11	10-23	?	?
60-120	?	?	?
45°	45°-60°	20°-45°	45°
4-8	8-13.5	8.5-10.5	4.5-8.5
20-30	12.5-18.5	12-14	9.9 ± 2.6
20-30	?	?	?
8-12	?	10-12	?
?	?	?	7.6 ± 1.54
?	40-42	?	?
?	2	?	?

published data), and for that species, prey are seasonally distributed within the year, and the hypothesis is that females should wait for a burst of prey availability to make nests. It is likely that prey abundance for *B. angulata* also exhibits seasonal variation, because many plant-feeding insects in this environment have strongly seasonal life cycles, and a similar explanation may apply here. It is alternatively possible, though questionable, that these excess females were nesting elsewhere but all foraging in a limited area together; i.e., the females sampled at the flowers represented the combined population of several nesting areas. However, this was not the only patch of suitable flowers in the area, and there is no obvious reason why the wasps would be concentrated in this particular patch.

Because we found no relationship between the number of nesting females and the average number of nests per female, we suggest that crowding has no effect on the number of nests made in the aggregation, despite the preference to nest in a somewhat limited area. It is also possible that females made only one or two nests in the aggregation and then dispersed to other areas, given that a female can live for up to 84 days, yet few were in residence this long. That is, rather than interpreting the small number of nests per female as a result of high mortality, there may be some undetected nesting activity outside of the known aggregation area; further work with marked females might help resolve this. In either case, the availability of adequate patches (whether aggregations form in them or not) may be of primary importance in the nesting dynamics of this species. In addition to other forces that could potentially influence nesting dynamics is the frequent extirpation of nests or entire aggregations by termites and ants, and the high frequency of nest desertion, due to several causes. Therefore, the patchiness of the environment and the dynamics within the aggre-

gations are likely to be crucial in the population dynamics of this species.

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